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RONN W. COLDIRON¹

ABSTRACT

A new individual of *Acroploous vorax* is described and its systematic position within the Saurerpetontidae is reexamined. The new specimen is clearly conspecific with the type as shown by narrow midline elements, broad supratemporal and intertemporal, wide but short lacrimal, and nearly identical pterygoids.

The new specimen offers more data on the brain-case, pterygoid occiput, lower jaw, and humerus. The internal process of the pterygoid is small and a well-developed epipterygoid caps the dorsal process of the pterygoid, indicating a more primitive basal articulation than that interpreted for *Isodectes*. Unfortunately, the condition in *Saurerpeton* is unknown for comparison. Like all other saurerpetontid genera (*Dvinosaurus*, *Saurerpeton*, *Isodectes*) the lower jaw has a large symphyseal tusk and a long retroarticular process. The new material, however, is primitive in having a small posterior meckelian fossa. Advanced

lower jaw characters are an overall dorsoventral compression and a unique wide exposure of the articular both laterally and medially. The vertebrae are unique among saurerpetontids in having a cartilaginous portion of pleurocentrum conspicuously larger than the intercentrum.

A hypothesis of relationships suggests *Acroploous* to be the sister group of *Isodectes* and brachyopids. As a result the saurerpetontids are paraphyletic since they exclude the brachyopids. Further, if brachyopids are the sister group to "saurerpetontids" and other stereospondyls are more closely related to eryopids, then stereospondyls would be diphyletic. There are many characters, however, that contradict the hypothesis of stereospondyls being diphyletic. *Dvinosaurus*, long thought to be an aberrant member of the trimerorhachoids, is thought to be the sister group to "saurerpetontids" and brachyopids.

INTRODUCTION

In 1971 Orville Bonner and Larry D. Martin reopened the quarry at Keats, Kansas, in which the type of *Acroploous vorax* Hotton was discovered. The following year Steven Dart and Bonner nearly finished quarrying operations. More material of this saurerpetontid amphibian was recovered and is described here (fig. 1).

Besides the *Acroploous* material other labyrinthodont types, a lungfish, and possible microsaur remains, were discovered. During the summer of 1974 I worked the remainder of the producing layer at Keats.

Since Hotton (1959) described *Acroploous*, Chase (1965) reviewed the known members of

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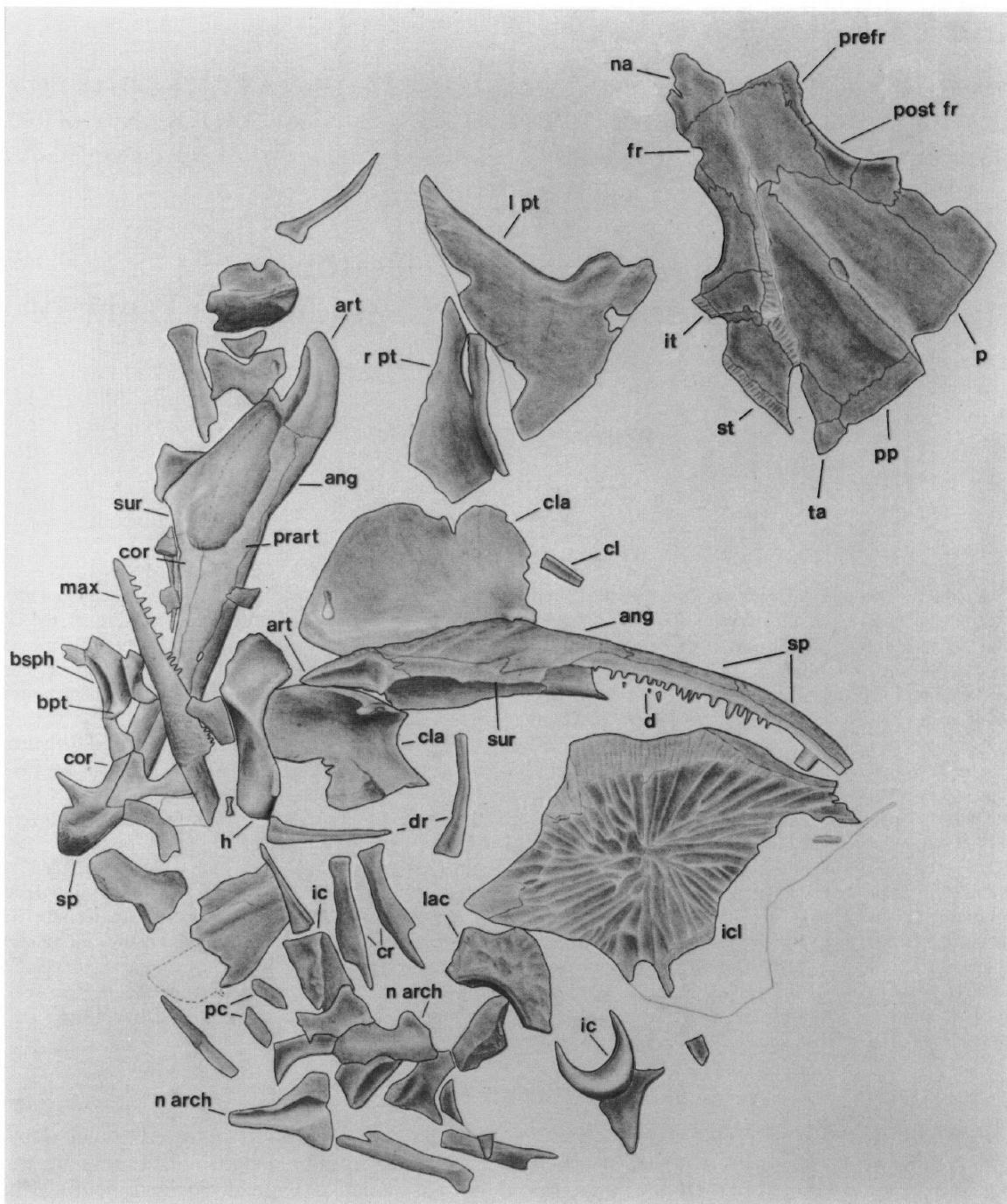


FIG. 1. View of main block of new specimen of *Acropelous vorax* Hotton (KU 28352). $\times 1.6$.

Abbreviations: *ang*, angular; *art*, articular; *bpt*, basipterygoid process; *bspf*, basisphenoid; *cl*, cleithrum; *cla*, clavicle; *cor*, coronoid; *cr*, cervical rib; *d*, dentary; *dr*, dorsal rib; *fr*, frontal; *h*, humerus; *ic*, intercentrum; *icl*, interclavicle; *it*, intertemporal; *lac*, lacrimal; *l pt*, left pterygoid; *max*, maxilla; *na*, nasal; *n arch*, neural arch; *p*, parietal; *pc*, pleurocentrum; *postfr*, postfrontal; *pp*, postparietal; *prart*, prearticular; *prefr*, prefrontal; *r pt*, right pterygoid; *sp*, splenial; *st*, supratemporal; *sur*, surangular; *ta*, tabular.

the Trimerorhachoidea and reclassified the group. Baird (personal commun.) and Welles and Estes (1969) dealt with the possible relation of *Isodectes* (*Eobrachyops* Watson) to the brachyopids. Olson and Lammers (1976) have described a form, *Kourerpeton*, also closely related to the brachyopids. The new material adds much information about the morphology of *Acroploous* and suggests that it is more closely related to *Isodectes*, *Kourerpeton*, and the brachyopids than to any other known member of the Trimerorhachoidea.

I thank Drs. T. H. Eaton and L. D. Martin for their guidance while this work was first undertaken at the University of Kansas. Mr. Orville Bonner was a great help through his fine preparation of the new material. Dr. Donald Baird of Princeton University deserves many thanks for lending his time and advice concerning his recent work on *Isodectes*. I thank Dr. Eugene Gaffney of the American Museum of Natural History for suggestions for revision of the manuscript. Ms. Michèle Coldiron was indispensable in typing the manuscript. Mr. Chester Tarka and Ms. Lorraine Meeker helped with the illustrations. Lastly, I thank Mr. Raymond Schurle for permission to work at the Keats locality.

GEOLOGY AND AGE OF THE SEQUENCE

The locality is on the farm of Raymond Schurle in SE $\frac{1}{4}$ NW $\frac{1}{4}$, Sec. 36, T9S, R6E of Riley County, Kansas. The Speiser Shale forms nearly all of about 20 vertical feet of a steep bank along Kitten Creek. The exposure runs along the stream for 72 feet just north of Keats. The exposure faces S50W.

The Speiser Shale is bracketed by the Funstone Limestone below and the Threemile Limestone above. The Funstone forms the stream bed and the Threemile caps the stream bank. The Speiser is a series of alternating 2- to 4-feet thick red and green shales. Very thin (2 inches) gray-green limestone sheets lie between only a few of the red and green shale facies. The producing layer is gray-green and lies 4 feet above the Funstone Limestone. Immediately below the producing layer is a well-indurated red facies. The contact between these two facies is marked by small pockets of green shale penetrating the topmost part of the red

layer. Quite often vertebrate remains are found in these pockets. A 2-inch iron-stained green shale lies above the producing layer followed by a 1-foot thick light green shale.

Most recently the Gearyan stage has been considered to form the base of the Permian in Kansas (Zeller, 1968). Dunbar et al. (1960) placed the Speiser Shale near the Putnam-Admiral Formation boundary, Wichita Group, Texas. Hotton (1959) preferred to correlate the Speiser Shale with the upper part of the Pueblo Formation. The Pueblo Formation lies at the base of the Wichita Group, Permian System of north-central Texas. Thus, Hotton compared the Speiser with the lowest vertebrate bearing beds of Texas. This comparison was based on the similarities to *Saurepeton* and "Pelion" of the Pennsylvanian (Upper Freeport) and "*Eobrachyops*" of the Permian (Arroyo, Clear Fork Group).

Baird (in Welles and Estes, 1969) synonymized "*Eobrachyops*" from the Texas Permian with *Isodectes* from the Pennsylvanian of Kansas (Bern Limestone, Wabaunsee Group). Hotton's attempt to compare the Speiser Shale to the Texas Permian (Pueblo) on the basis of vertebrate similarities is no longer feasible. *Isodectes* (*Eobrachyops*) ranges too far stratigraphically to be of use in correlation.

Clendening (1971) placed the Gearyan Stage of Kansas entirely within the upper Pennsylvanian Series. He used palynological evidence to show that "Gearyan age spores and pollen demonstrate no profound change from the underlying Virgilian" (Pennsylvanian). Only when one reaches the Wymore Shale (Chase Group—overlies the Speiser Shale, Council Grove Group) does bisaccate pollen increase significantly. Wilson and Rashid (1971) by using palynological evidence also reached the same conclusion that the Gearyan stage is Pennsylvanian in age.

However, all of these sediments were deposited in a lowland environment, far away from the Arbuckle highlands in Oklahoma. Langenheim (1952) stated "lowland plants become known as Pennsylvanian indices in the mid-western and eastern United States." In that part of the country "during the Pennsylvanian . . . uplands did not exist . . . as the seas were obliterated in the Permian, however, more up-

land plant material found its way to the sites of deposition and was fossilized." Because the Gearyan sediments in Kansas were far away from any uplands one might expect only Pennsylvanian pollen assemblages. One is left with equivocal evidence as to where to place the Permo-Carboniferous boundary in the midcontinent.

SYSTEMATIC DESCRIPTION

CLASS AMPHIBIA

ORDER TEMNOSPONDYLI

SUBORDER RHACHITOMI

SUPERFAMILY TRIMERORHACHIOIDEA

FAMILY SAURERPETONTIDAE CHASE, 1964

GENUS *ACROPOLOUS* HOTTON, 1959

AMENDED DIAGNOSIS (largely from Hotton, 1959): A typical saurerpetontid amphibian, having a short face, extremely reduced otic notch, well-developed retroarticular process, deep cheek, pronounced ventrally directed quadrate process of pterygoid, backward sloping occiput, and narrow tabulars. Parasphenoid articulates with broad ventral shelf of pterygoid. The following characters are unique for *Acropolous* and distinguish it from all other saurerpetontid genera: dermal midline elements narrow, large external nares, weak internal process of pterygoid; tabulars excluded from otic notch by supratemporal; wide lateral exposure of splenials; larger pleurocentra than intercentra; anterior border of interclavicle deeply pectinate.

Acropolous vorax Hotton, 1959

DIAGNOSIS: Same as for genus.

MORPHOLOGY

Nearly all the skull roofing bones preserved are exposed in ventral view, whereas only the lacrimal, parts of postparietal, and tabular are exposed dorsally. The parietals, postparietals, supratemporals, intertemporals, prefrontals and postfrontals, tabulars, nasals, and frontals are all partially articulated with each other. The left side of the skull has been disturbed so that the supratemporal, intertemporal, and postfrontal

are displaced slightly away from the midline elements. This displacement has exposed remarkably well-developed lappets which extended over their midline neighbors. Throughout the description of the skull roof these lappets will be described in detail so that a dorsal view of the skull roof can be reconstructed (fig. 2). The back margin of the skull is broken away from the occiput just anterior to the occipital crest.

NASAL: The nasals are the most anterior skull roofing bones preserved. The bones end laterally in a broken edge. Medially a moderate lappet (0.5 mm.) overlies the adjacent (left) nasal in dorsal view. Posteriorly the nasal forms a moderately deep wedge between the prefrontal and frontal bones. This wedge marks the beginning of the midline elements. *Saurerpeton* has a broad posterior wedge but no constriction of the frontals or parietals follows. In *Acropolous* the posterior facing wedge of nasal interingers deeply with both frontal and prefrontal. Thus, a strong sutural union is formed with all adjacent bones that are preserved. The anterior portion of the bone has been lost.

In both the type and referred specimens the nasal extends posteriorly to a point level with the first one-quarter of the orbital diameter. In

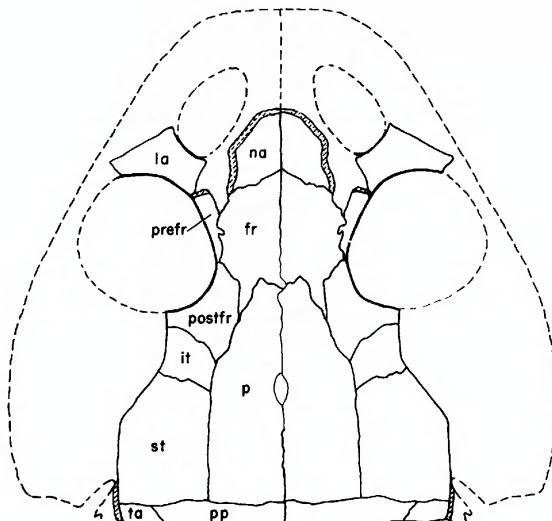


FIG. 2. A reconstructed dorsal view of the skull roof. Right and left sides of skull are mirror images; hatched areas indicate an element is incomplete. Abbreviations as in figure 1. $\times 1.2$.

all other saurerpetontids the posterior margin of the nasal lies anterior to the orbital border. In *Dvinosaurus* (Bystrow, 1938) one or both nasals reach the anterior level of the orbits.

PREFRONTAL: The prefrontal ends anteriorly in a break where the orbits begin to turn dorsolaterally. Thus, only a posterior bar is preserved around the orbit while its anterior widening has been lost. Medially the prefrontal interfingers with both nasal and frontal. Parts of the suture form a lock-and-key coupling which further reinforces the strong suture. Posteriorly the bone remains at a fairly constant width (1.5 mm.) until the postfrontal boundary is reached. Here, the bone has narrowed to 0.5 mm. and interfingers deeply with the postfrontal. This posterior constriction is typical of all saurerpetontid genera except *Isodectes* where the prefrontal maintains a constant width. Because of the deep interfingering of this element a large medially directed lappet over the frontal is thought not to be present. The posterior constriction, then, probably exists in dorsal view as well. The lateral margin of the bone is thickened to form a rounded ridge under the dorsal rim of the orbit. The anteriomost part of this ridge is sheared to show itself in cross section. This break is facing slightly ventrally (from a dorsal perspective) which shows the face began to turn downward at the anterodorsal margin of the orbit.

POSTFRONTAL: The postfrontal is bounded anteriorly by the prefrontal, laterally by the frontal and parietal, and posteriorly by the intertemporal. The lateral boundary is taken up almost entirely by the orbit. Farther posteriorly the edge is broken so that the postorbital contact is lost.

The right postfrontal has been displaced to the left (in ventral view) and the underlying parts of frontal and parietal have been destroyed by a crack running roughly parallel to the suture between these three bones. The suture with the prefrontal has been described above. The anterior one-third of the postfrontal interfingers with the frontal in a complicated fashion. Posterior to this point a lappet develops with increasing width to the juncture with the intertemporal. This lappet is well preserved and consists of parallel posteromedially pointing ridges which fitted over the frontal and

parietal. The postfrontal-intertemporal suture is relatively straight where the lappet begins. The lappet type of suture must also have reinforced the skull like those of the interfingering type.

Because of the overlapping of frontal by postfrontal the shape of the postfrontal is somewhat different from dorsal aspect. From a ventral view the bone curves posterolaterally around the dorsal rim of the orbit. The bone steadily increases in width posteriorly as the medial border gently curves posterolaterally. When seen from a dorsal view, however, the postfrontal is wider and impinges on the posterior half of the frontal. The lappet of the postfrontal reaches its maximum width at its posterior margin. This causes a posteromedial turning of its dorsal margin over the anterior-most part of the parietal. The exact shape of the flange over the parietal cannot be determined. However, the development of the lappet posteriorly agrees with the appearance of a flange in the type specimen. These medially directed lappets further contribute to the constriction of midline elements which started at the nasals. Also, the portion of lappet overlying the parietal indicates a much wider postfrontal-parietal contact than does the type specimen. In general this new specimen is more typical of other trimerorhachoids. This posterior expansion of the postfrontal is similar to other saurerpetontids except *Saurerpeton*. The postero-lateral margin of the bone is broken so that a lateral flange in the type cannot be determined for the specimen at hand. The orbital margin is swollen to form a ridge around the under surface of the orbit as does the prefrontal.

INTERTEMPORAL: The intertemporal-postfrontal border is straight, and the two bones are separated by about 0.25 mm. Any interfingering of this suture could be masked by a fracture along the suture. Medially, there is a well-developed lappet, 1.5 mm. wide, which is continuous with the more anterior lappet of the postfrontal. Laterally, a lappet is also present which overlies the postorbital. The edge of this lateral lappet is gently concave and agrees with a similar convex postorbital-intertemporal border in the type specimen.

The posterior border is a simple suture but complicated by fractures and subsequent displacement. A lappet can be seen between the

intertemporal and supratemporal. The displacement is small (0.5 mm.) so that neither the width of the lappet nor which bone it overlaps can be seen. Also, parts of the posterior margin of the intertemporal are fractured which obscures the shape of its ventrally exposed suture. Because displacement between the postfrontal and intertemporal is slight no overlapping can be seen if present.

Like that of the type, the intertemporal in dorsal view must be a very large rectangular bone with relatively simple borders. Its posterior border runs posteromedially as does the same border of the type. The posterior suture trends posteromedially. Because no lappet can be seen anteriorly, a concave anterior border (apex pointing anteriorly) cannot be determined.

Compared with other saurerpetontids the intertemporal is quite large. Its squarish outline resembles only that of *Isodectes* but the element in that genus is much smaller.

SUPRATEMPORAL: The supratemporal is also a large rectangular element with a broadly pointed anterior border. Among other trimerorhachoids, the element most resembles *Saurerpeton* and *Trimerorhachis* in its long but narrow proportions. The supratemporal of *Neldasaurus* is also long and narrow but does not take up as great a proportion of the skull table as in the former genera. Description of the lateral and medial lappets of the supratemporal allows an estimation of small otic notch size and cheek-skull table kineticism. These lappets are well developed and overlie the parietal and squamosal. The sutural reinforcement by the lateral lappet over squamosal would allow no movement between these two elements. Ridging of these lappets is seen clearly in ventral view. The lateral lappet is 1.0 mm. wide, whereas the medial lappet is 1.5 mm. wide. The lappet on the right supratemporal is broken off at the posterior one-third of the bone length. The right supratemporal shows that the lappet extended at least to the posterolateral edge of the bone. This lateral lappet overlies the supratemporal along its entire lateral edge. The otic notch, then, could not have extended farther along the cheek than the anterior margin of the tabulars (which are thin anteroposteriorly). Only *Dvinosaurus*, *Isodectes*, *Kourer-*

peton, and the brachyopids have decreased the otic notch to a greater degree, whereas *Saurerpeton* and other trimerorhachoids maintain a larger one.

TABULAR: The tabulars are broken both laterally and posteriorly. The anterior and medial sutures with supratemporal and postparietal can be seen only on the surface where the bones abut against each other. The wide medial lappet of supratemporal restricts the dorsal exposure of tabular to a more lateral position, farther from the parietals. This condition exists in the type specimen and is very similar to that seen in *Isodectes* and *Dvinosaurus*. However, in both cases the tabular is reduced to a narrow strip so that the separation from the parietal is more lateral than posterior as in *Saurerpeton*, *Trimerorhachis*, and *Neldasaurus*.

The tabular forms the dorsolateral border of the occiput. This part of the bone forms a right triangle with the apex pointing laterally. A small sheet of bone projects ventrally, anterior to the apex of the tabular. Hotton (1959) assumed this sheet of bone comprised the anterior margin of a posttemporal fenestra. If this part of the tabular received a cartilaginous paroccipital process, the posttemporal fenestra would lie medial to this tabular process. Posterior to the ventrally directed process, the tabular is folded to form a dorsally directed pit.

In every way, the occipital exposure of the tabular is comparable with those of *Dvinosaurus* and saurerpetontids. In all these genera the posttemporal fenestra is small and lies medial to a ventrally directed tabular process. Unfortunately the condition in *Saurerpeton* is unclear.

POSTPARIETAL: Both postparietals are nearly complete, with the left attached to the occiput. The right postparietal is broken at the occiput-skull table juncture. A gentle serrate suture exists with the parietal and runs at right angles to the midline. The subcutaneous portion forms a long, thin rectangular element as in the type specimen, and unlike any other trimerorhachoid. However, there is no medial expansion anteriorly toward the parietals, which does occur in *Dvinosaurus* and *Isodectes*.

A prominent ridge separates the skull table from the occiput. The ridge expands ventrally toward the midline to form an inverted triangu-

lar area of thickened bone. The suture between postparietals runs down the center of the triangle and ends at a space occupied by the missing supraoccipital. This triangular ridge is unique among the saurerpetontids although a pillar-shaped ridge occurs in *Dvinosaurus* and *Isodectes*. More ventrally and laterally, the postparietal overlies the exoccipital in a straight, horizontal contact.

Immediately above and lateral to the exoccipital the postparietal interdigitates with the tabular. This suture runs dorsolaterally toward the skull roof. As a result the postparietals occupy most of the dorsal half of the occiput. This wide occipital exposure of the postparietals is characteristic of trimerorhachoids in general.

PARIETAL: The parietals are nearly identical in shape with those in the type. Posteriorly, the parietals are comparable with other saurerpetontids in width but converge to form a narrow union with the frontals. In the specimen at hand, the frontal-parietal suture is uncertain. Two breaks on either side of the parietals might represent its anterior border. These two are relatively close together and are different from the frontal-parietal juncture in the type. The new specimen shows this suture tending antero-medially rather than at right angles to the midline in the type. The bones probably interfingered with one another so that a lappet is unlikely. A lappet could change the dorsal limits of the parietal, but the union between parietal and frontal could still be longer and somewhat wider. If differences do exist in the parietal-frontal union they need not be significant because the new specimen is larger than the type.

The parietals extend anteriorly to at least the posterior one-third of the orbit and possibly one-half of its length. The parietals of the type extend only to the posterior limit of the orbit. This difference may also be due to the size difference between the two individuals. Only in *Saurerpeton* does the parietal extend as far anteriorly. This similarity may not be significant because of possible changes in relative proportions due to comparison of different growth stages.

The midline suture is of simple abutment type along most of the parietal and frontal

length. There is slight interfingering between parietals posterior to the parietal foramen. This opening is situated more anteriorly in the new specimen. In ventral view an elongate oval pit (1.5 mm. long) appears to communicate posteriorly with the parietal foramen.

FRONTAL: The frontal has a general rectangular shape with a swollen lateral margin where it meets the relatively narrow prefrontal. If the interpretation of the dorsal view of the skull roof is correct, only the posterolateral portion of the bone reaches as far posteriorly as it does in the type. Except for the midline suture the frontals are united with their neighbors by strong sutural contacts (lappets or complex interfingering) which have been described above.

Relative to other trimerorhachoids only *Trimerorhachis* has comparably short prefrontals. By far, the prefrontals of both the type and the referred specimen of *Acroploous* are narrower than any other trimerorhachoid.

LACRIMAL: The right lacrimal lies alone and is exposed in lateral view. Well-developed random pits and ridges present themselves clearly. A deep furrow traverses the orbital margin of the lacrimal anteroventrally. Nearly all the bone is present, which is roughly L-shaped. The orbital margin of the bone subtends an angle of approximately 90 degrees, which is greater than the exposure in the type. The narial border lies only 5 mm. from the anterior end of the orbit, and a wide concave border, although unbroken, clearly indicates a large narial opening. The lacrimal makes up the entire back margin of the naris. Although the face is poorly represented, the enlarged naris and its short distance to the orbit point toward an attenuated face with the bones crowded as in the type. Only in *Dvinosaurus* and *Saurerpeton* among trimerorhachoids does the lacrimal enter both the orbit and naris while maintaining its characteristic shortness. In *Isodectes* the lacrimal resembles the brachyopid condition in not reaching the naris.

A thin smooth shelf on the dorsolateral surface marks the area of overlap by the dorsally expanded maxilla. This smooth shelf is downturned so as to point nearly vertically in natural position. The naris lies above this downturning so that most of the orbit, the naris, and most of

the lacrimal lie at about a 45 degree angle to the horizontal midline elements. The bone narrows posteriorly to present only a thin contact with the prefrontal.

MAXILLA: The left maxilla is dissociated from the rest of the skull and lies over the right lower jaw. Twenty teeth are visible with space for 10 to 14 more. The teeth gradually decrease in size posteriorly. The anterior teeth are approximately 0.9 mm. in height, whereas the posteriormost decrease to 0.6 mm. in height. The maxilla is broken so that the narial border is missing dorsally. The bone as preserved is 22 mm. in length, and is similar in length to *Isodectes* but shorter relative to skull length in *Dvinosaurus* and *Saurerpeton*. If the maxilla ends under the posterior end of the orbit the anterior margin extends just ventral to the naris. The length of this maxilla agrees well with that of the type. Unlike the type, the posterior part of the new maxilla does not curve ventrally as the beginning of the down-turned cheek.

BRAINCASE

IMPRESSIONS ON THE SKULL ROOF: There are distinct impressions of the dorsal braincase margins running longitudinally along the parietal bones. Near the postparietal-parietal boundary, the braincase impression is widest. From its posterior end the impression gently curves anterolaterally to a maximum width of 3.0 mm. The border then curves sharply medially toward the parietal foramen to form a distinct waist. The edge of the waist forms a right angle. From the waist, the impression runs anteriorly and slightly laterally at a constantly increasing width in the sphenethmoid region. The impression disappears toward the anterior border of the parietals.

The dorsal margin of the braincase appears to be narrow because its borders are totally confined to the medial half of the parietal width. A narrow braincase is presumed by Romer (1947) to indicate a primitive condition. The platybasic type is characteristic of more advanced temnospondyls. Unfortunately the condition in other saurerpetontids is unknown.

BASISPHENOID: The basisphenoid, although incomplete, is the only one reported among the saurerpetontids. The element is exposed ventrally so as to show part of the right basipterygoid process, a waist immediately behind the process, and diverging lateral walls both anteriorly and posteriorly. The bone is 3.0 mm. high. The dorsal half of the right lateral wall extends 3.5 mm. anterior to the basipterygoid process and 2.0 mm. posterior to the broken ventral edge. This part of the wall is crushed and pushed slightly outward. No foramina are visible.

The right basipterygoid process points anteriorly at a 40 degree angle from the midline. The articulating surface is oval and directed dorsolaterally. The surface is unfinished so that the process must have been finished in cartilage. A groove courses over the process at its base dorsally. A ridge runs back from the basipterygoid process along the lateral edges of the ventral surface. A shallow trough results with the ridges forming the lateral walls. The trough wall is thickened between the basipterygoid processes but the floor thins posteriorly.

Although crushed and displaced laterally, the dorsal half of the lateral wall was more vertical in life. The part extending past the basipterygoid process would then bend anteromedially. This anterior arm when joined with its partner forms the posterior portion of the sphenoid. A vertical break above and slightly behind the basipterygoid process may represent a suture between the sphenoid and the basiphenoid.

The basipterygoid processes are 6 mm. apart when measured at their lateralmost edges. Up to 4 mm. more in width could be occupied by the cartilaginous part of the processes. Adding another 8 mm. for the horizontal shelves of the pterygoid (at the internal process), the total width allowed for the wings of the parapphenoid is approximately 18 mm. This measurement agrees quite well with the width of parapphenoid wings of 20.0 mm. Allowing that the specimen at hand is larger than the type, the width of the parapphenoid wings agree quite well.

OCCIPUT: All the elements of the occiput are

present and in near perfect articulation (fig. 3). The occiput and posterior part of the skull table are crushed on the same plane. The occiput could slope more than 50 degrees backward from the horizontal, which is at least 30 degrees greater than the angle in *Kourerpeton*. The occipital angles found in brachyopids are intermediate between *Kourerpeton* and *Isodectes* (40° to 20° from horizontal). In *Acropolous* the posteriormost extent of the exoccipitals reaches 5 mm. back of the skull table.

The basioccipital is poorly ossified, and this portion does not protrude posteriorly from the occiput. The supraoccipital is completely unossified, but a broad space wedges between the postparietals and indicates its presence in cartilage.

BASIOCCIPITAL: The basioccipital consists of two ventrally oriented fingers of bone wrapped around the back of the parasphenoid. These two processes barely meet at the midline, thus excluding the parasphenoid from an occipital exposure. Dorsally, the basioccipital is deeply recessed and is of unfinished bone.

Exclusion of the parasphenoid from the occiput is a primitive feature among temnospondyls although *Isodectes* and brachyopids show the advanced condition in which the parasphenoid breaks through to the occipital surface. The condition in *Dvinosaurus* is unclear. In ventral view some of Bystrow's (1938) figures show the basioccipital excluding the parasphenoid from the occiput. In occipital view, Bystrow's figure 5 shows the parasphenoid well exposed.

EXOCCIPITAL: The exoccipitals form the lateral and ventrolateral borders of the broad oval-shaped foramen magnum. Ventrally, the foramen magnum is open. Two narrow arms of the exoccipitals face each other on the ventral margin but do not meet. The basioccipital could have contributed to the ventral margin, or the arms of the exoccipital could have met in cartilage. The type specimen is more incomplete in this region and does not help clarify the matter.

In occipital view, the exoccipital has a wide contact with postparietal and tabular and narrows ventral to the foramen magnum to form an unfinished posteroventrally directed condylar surface. This condylar surface is unfinished so that it must have been continued in cartilage. The posteroventral orientation of the condyle and its long posterior projection indicate that it contributed at least to the dorsolateral part of the occipital condyle. Because of the poor ossification of the basioccipital, it cannot be determined what part it contributed to the occipital condyle. If the contribution of the basioccipital was small, the occipital condyle could have been double.

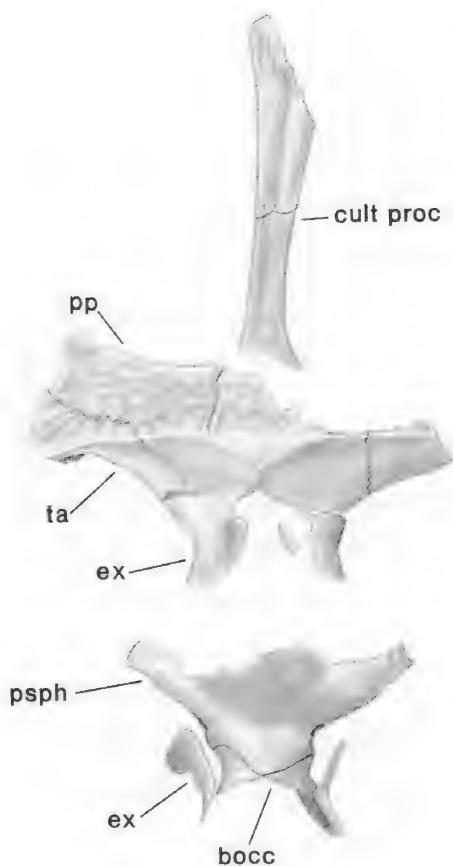


FIG. 3. Top—back of skull roof, occiput, and cultriform process of paraspheonoid in dorsal view. $\times 1.5$. Bottom—ventral view of same block showing the main body of paraspheonoid and occiput. $\times 2.1$.

Abbreviations: *bocc*, basioccipital; *cult proc*, cultriform process of paraspheonoid; *ex*, exoccipital; *psph*, paraspheonoid; *pp*, postparietal; *ta*, tabular.

In ventral view the exoccipital laps over both parasphenoid and basioccipital. The bone then turns vertically to form a flat lateral wall. The XII cranial nerve pierces the lateral wall anterodorsally near the contact with the postparietal. The nerve may have turned dorsally and posteriorly into a canal which exits the exoccipital ventral to the foramen magnum. No evidence for a vagus foramen can be detected. The exoccipital is compared more fully with other trimerorhachoids in the discussion.

Opisthotic and prootic bones are missing or were not ossified.

PALATE

The palate is represented only by the pterygoid and parasphenoid. Both right and left pterygoids are present with the left exposed laterally and the right medially. Both are essentially complete. The anterior and posterior ends of the right pterygoid are buried under the left pterygoid and left clavicle, respectively.

PTERYGOID: Palatal, quadrate, and ascending rami make up the pterygoid. The palatal ramus has only a thin horizontal shelf running from near its tip to the middle portion of the bone. At its tip the shelf gradually turns ventrally and points ventrolaterally at 45 degrees. More posteriorly the shelf turns abruptly ventrally to form a vertical wall. The vertical shelf increases steadily in depth posteriorly to just below the epipterygoid. The palatal ramus is 18.1 mm. in length. The quadrate ramus dips steeply to further deepen the vertical shelf. The quadrate ramus is short (9.2 mm.) and bends only slightly laterally toward the back margin of the cheek. The sharp downturning of the quadrate ramus must have made the cheek at least moderately deep as in *Isodectes*, *Kourerpeton*, and the brachyopids.

The posterior margin of the pterygoid is nearly vertical and extends upward and forward to the epipterygoid. Broken sheets of bone overlap the ascending ramus of the pterygoid and may represent parts of the epipterygoid. The ascending ramus together with the epipterygoid and ascending ramus of the pterygoid point anteromedially at 45 degrees to the palatal ramus. A posteromedially facing recess lies

at the anterior edge of the ascending ramus (and epipterygoid?). Posterior to this recess the ascending ramus rises 3.5 mm. A low broad ridge separates the recess from the higher portion of the ascending ramus.

In natural position the recess would cover only the anterior portion of the basipterygoid process. Because the extent of the epipterygoid is unclear it is difficult to determine how much it contributes to the basal articulation. However, the articulation was certainly movable and the epipterygoid must have played a part. The condition in other saurpetontids is unknown due either to lack of preservation or ossification. *Trimerorhachis* presumably maintained the primitive condition (Romer, 1947).

The internal process of the pterygoid projects only 1 mm. medially, below, and slightly forward of the recess on the dorsal ramus. The maximum width of the horizontal shelf from the internal process to the vertical wall is only 3.0 mm. It would be difficult to accommodate a long lateral wing of the parasphenoid. However, a horizontal shelf indicates that there was a dorsal covering over the parasphenoid as in *Dvinosaurus* and *Isodectes*. Therefore, the basal articulation between the dermal elements must be essentially the same. This shelf is covered more fully in the discussion below.

The relation of the dorsal and quadrate rami to the squamosal, quadratojugal, and quadrate bones is unclear. The thickness and height of the dorsal ramus certainly indicates a union with the supratemporal-squamosal area in front of the otic notch. The posterodorsal margin of the ascending ramus curves slightly laterally and could have lapped over the squamosal. Unlike the type specimen, there is no shagreen of palatal teeth on the medially exposed right pterygoid.

PARASPHENOID: The parasphenoid is nearly complete with the anterior half of the cultriform process left as an impression. The cultriform process gradually widens anteriorly to a maximum width of 7 mm. This width is comparable to the relatively wide cultriform process found in other saurpetontids. At its anterior expansion, faint grooves cut into the ventral surface which mark the contact with the vomers. In life this contact was probably mova-

ble because of complete separation of the parasphenoid and anterior portion of the palate. The cultriform process is marked by a median ridge running along the ventral surface.

At the base of the cultriform process, the borders turn abruptly and at right angles laterally to form the anterior edge of the parasphenoid wings. This anterior border is slightly concave. The wing terminates laterally in a blunt tip 2 mm. wide. The leading edge of the wing is of reasonably thickened bone. Reinforcement of the leading edge suggests the parasphenoid wings articulated with the horizontal shelf of the pterygoid, and thus contributed to the basal articulation. The basal articulation, then, is composed of both pterygoid-parasphenoid and basisphenoid-pterygoid (plus epipterygoid) parts. This interpretation agrees with Hotton's (1959) for the type specimen.

The posterior border of the parasphenoid wings runs posteromedially to a broadly rounded end. The exoccipitals and basioccipital flank the entire posterior border. The body of the parasphenoid receives the exoccipitals in a shallow elongate depression just posterior to the wings. Farther posteriorly, the rounded end of the body is sutured to the ventrally directed wedge-shaped fingers of the basioccipital. The rounded end of the body has no open exposure to the occipital surface.

LOWER JAW

Both rami of the lower jaw are present. The left ramus is exposed in lateral view and is nearly complete and undisturbed. The right ramus affords a medial view and is crushed so that the lateral half is displaced slightly above the medial half. In both rami the bone is fractured badly in places but most sutures can be made out.

The ramus is slender anteriorly. Past the tooth row the dorsal margin swells to a maximum height near the dentary-coronoid junc-
ture. Farther posteriorly the jaw narrows gradually dorsoventrally. A long, strongly de-
veloped retroarticular process (7.5 mm.) ex-
tends past the glenoid fossa.

In cross section the anterior portion of the ramus is rounded with the bones below the

teeth forming a shallow U. Posteriorly, the jaw is more slender and higher in cross section but remains wide. Ornament is present mainly on the ventral half of the lateral surface and is moderately rugose. The lower jaw length affords much information about the skull length. The distance from the symphysis to the posterior end of the glenoid fossa is 53 mm. The distance from the "occipital crest of postparietal to snout" (Hotton, 1959) in *Acropelous* is 44 mm. All in all, the jaw is typical in general shape to that in any trimerorhachoid. Only in the anterior dorsoventral compression is it atypical.

The tooth row in the new specimen is more complete than the tooth row in the type. Twenty teeth are present in the left ramus with space for about 10 more. The teeth increase in size posteriorly to the ninth tooth (fifteenth if a complete row were present). Tooth size varies only slightly posterior to the ninth tooth. The largest teeth reach a height of 2.0 mm. The variation in tooth size cannot be studied with respect to replacement. Removal of matrix from around the fragile teeth would almost certainly destroy the tooth row. A tusk rises from the medial margin near the symphysis. All the teeth show shallow labyrinthine infolding of the enamel at their bases.

DENTARY: The dentary is a long, thin bone which occupied no more than one-third to one-half of the lateral jaw surface. *Acropelous* shows the primitive condition of narrow exposure of the dentary relative to *Trimerorhachis*, *Iso-
dectes* (Chorn, personal commun.), and *Saurer-
peton* (USNM 4471). The condition in brachyopids is variable as seen in Watson's (1956) figure 2 of *Bothriiceps* and Welles and Estes's (1969) figure 20 of *Hadrokkosaurus*. Ornament is lightly developed with only faint striations present. Posteriorly, the dentary is broken immediately in back of the tooth row. A jagged edge continues posteriorly to the front of the adductor fossa. This missing portion of the dentary begins to rise gently toward the coronoid process but wedges out below it. Medially, the bone is exposed only slightly.

SPLENIALS: The splenials have a noticeably pitted surface unlike the dentary. The bones are laterally exposed for about one-half the height

of the ramus. This wide exposure is primitive and its analysis is covered above in the description of the closely associated dentary. The orientation is nearly flat ventrally and only takes a shallow dorsal turn to meet the dentary. The result is a compressed anterior half of the jaw. The anterior splenial most probably shared in the jaw symphysis with the dentary. There is no sign of narrowing anteriorly. Both splenial and postsplenial are of equal length. The postsplenial meets the angular under the third tooth from the end of the tooth row. The splenials occupy one-third of the medial wall and lie under the coronoids. This is a relatively advanced condition and *Saurerpeton* (AMNH 6935), *Trimerorhachis*, and *Isodectes* (Chorn, personal commun.) have broad medial exposures as well. On the other hand, *Dvinosaurus* shows the primitive condition.

ANGULAR AND SURANGULAR: The posterior half of the jaw is badly fractured in lateral view. Parts of the sutures are obscured, and some of the bone surface is worn away. The surangular is restricted ventrally by a deep angular. The angular takes up approximately three-quarters of the lateral surface. In trimerorhachoids such as *Trimerorhachis* the angular is equally advanced in its dominance over the surangular. However, *Dvinosaurus*, *Saurerpeton*, and *Isodectes* are more primitive in having only a thin lateral exposure of the angular. The condition in brachyopids is variable as seen in *Bothriiceps* (Watson, 1956) or *Hadrokossaurus* (Welles and Estes, 1969). Medially, the angular covers a narrow longitudinal strip below the adductor fossa, like all trimerorhachoids for which the medial surface of the jaw is known. Dorsally, the surangular shares the anterior one-quarter of the coronoid process with the posterior coronoid. Medially, the surangular covers all but the anteriormost lateral wall of the adductor fossa.

PREARTICULAR: The prearticular covers the medial surface of the adductor fossa. Anteriorly, the prearticular extends past the small posterior meckelian foramen. Anterior to the meckelian foramen the element is obscured.

CORONOID: Only parts of the coronoids and splenials of the right ramus are exposed under overlying bone fragments. The coronoids occupy fully two-thirds of the medial jaw surface.

The splenials take up the rest. More posteriorly the coronoids bear a large number of closely packed denticles which run anteriorly to at least the middle of the tooth row. Toward the anterior end no denticles appear. The presence of denticles is a primitive rhachitomous feature which persists into the brachyopids (cf. *Hadrokossaurus*).

ARTICULAR: If the interpretation of the articular is correct, *Acropelous* would be unique among rhachitomous amphibians in having a wide lateral exposure. The articular meets the surangular dorsally about 3 mm. anterior to the glenoid fossa. Laterally, the suture runs posteroventrally, the articular meeting the angular below the anterior rim of the glenoid fossa. In medial view the suture runs vertically just posterior to the foramen chorda tympani. This foramen lies just anteroventral to the glenoid fossa.

The rim of the glenoid fossa forms a ridge of thickened bone dorsally and laterally extending back to the end of the retroarticular process. The fossa faces slightly laterally so that, articulated, the angular-surangular wall and adductor fossa lie vertically.

The retroarticular process is long and stoutly developed, as in all saurerpetontids and brachyopids. A groove runs dorsally along its entire length which must serve for insertion of part of the depressor mandibuli muscle. The well-developed retroarticular process, and long, deep adductor fossa point to an extremely strong jaw apparatus. The presence of reinforcing lappets of the dermal skull roofing bones goes in hand with the well-developed trigeminal musculature. As far as can be determined, nearly all bones of the lower jaw abut against or overlap their neighbors.

VERTEBRAE

The vertebral column is very fragmentary. Only a few vertebrae are present but all are well preserved and afford different views of the separate elements.

NEURAL ARCH: The neural arch (fig. 4a) measures 11 mm. in height and 5 mm. in width from a line running horizontally through the anterior zygapophysis. Immediately dorsal to this process the arch constricts to a waist 2.5

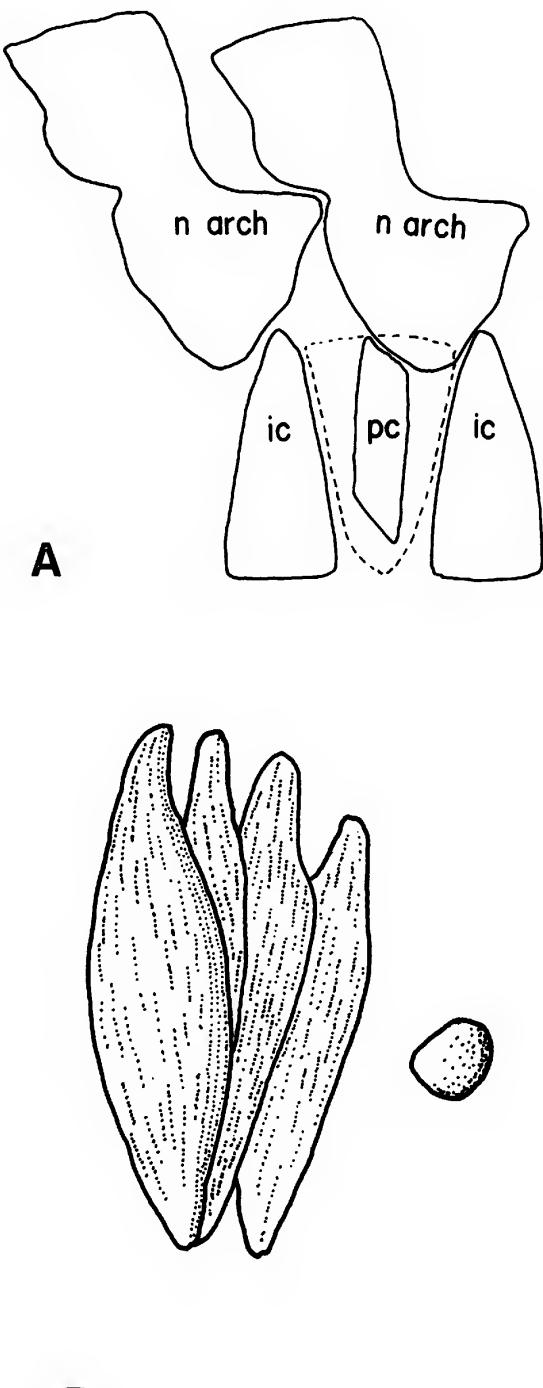


FIG. 4a, b. a. Reconstruction of vertebrae. Dotted line indicates probable cartilaginous extension of pleurocentrum. Abbreviations as in figure 1. $\times 3.5$. b. Scales reconstructed from fragments. One osteoderm shown at right. $\times 14$.

mm. wide. The dorsal edge of the spine slopes downward anteriorly and is 3.5 mm. wide.

The pedicel is a broad triangular element. The posterior surface runs nearly directly vertically. The anterior margin is wavy and runs anterodorsally at 45 degrees. There is no transverse process on the pedicel. The bone is smooth with very little relief. Only a small notch separates the zygapophysis from the pedicel. The anterior zygapophysis extends forward nearly 3 mm. from the anterior border of the arch. The posterior zygapophysis is poorly preserved but forms a flat articulating surface at least 1.4 mm. long. This surface leads into a notch that forms the posterior part of the waist. Dorsally, the zygapophysis is set off from the spine as a low bump. The neural arch resembles the dorsals of *Neldasaurus* and *Dinosaurus* in having fairly well-developed posterior zygapophyses and simple rectangular neural spines. These features seem to be primitive for rhachitomes.

In end view the pedicels expand ventrally, posteriorly, and laterally to form two triangular shaped areas of bone. This posterior expansion must have reinforced the rib articulation. Anteriorly, the pedicel wedges out to a sheet of bone. Posteriorly, there is only a small indentation for the nerve cord. Dorsal to the pedicel the arch narrows rapidly to form a narrow spine. Just dorsal to the posterior zygapophysis lies a shallow pit which must have served as an origin for an interspinous ligament.

INTERCENTRUM: The intercentrum is a broad U-shaped element, as in most rhachitomes. It is 3.2 mm. long ventrally. Dorsally, the bone constricts slowly to a narrow wedge. The element is 6.9 mm. high and the ascending processes barely point toward one another. The external surface is featureless except for two ridges running dorsoventrally along the borders. There is no indentation for reception of the rib capitulum.

PLEUROCENTRUM: The pleurocentra appear very much like the type. They are 4.0 mm. high and 1.5. mm. wide. Very little surface relief is present with only a very slight indentation on the posterior edge for articulation with the rib capitulum. The bone is of only moderate thickness unlike the relatively stout intercentrum. The anterior and posterior edges are

parallel. Both dorsally and ventrally, the edges converge to a point. Overall, the element resembles a long parallelogram.

Nearly all the vertebral elements are disarticulated, but reconstruction is not difficult because of the excellent preservation. Three nearly complete neural arches are exposed in lateral view. Two lie adjacent to each other and a third is far removed. Two fully exposed intercentra, one in lateral and the other two in end view, are used for the reconstruction. Only one pleurocentrum is adequately preserved to assist in the reconstruction.

The neural arch points backward at an angle of approximately 27 degrees from the vertical. At this angle, the anterior and posterior zygapophyses lie horizontal and are in wide contact (1.4 mm. overlap). The pedicel forms a wide ventrally pointing wedge and abuts against the anterior surface of the pleurocentrum. A slight concavity in the anteroventral edge of the pedicel receives the ascending process of the intercentrum.

The ossified portions of the central elements are of unequal size, with the intercentrum conspicuously larger than the pleurocentrum. However, because of the great width of the pedicel and backward pointing neural arches, the pleurocentrum must have been continued in cartilage to a greater overall size than the intercentrum (fig. 3). When in natural position the two elements contribute to supporting the arch very much like some dissorophids (*Doleserpeton*) and unlike other trimerorhachoids.

PECTORAL GIRDLE

A nearly complete interclavicle, two partial clavicles, and a fragment of a cleithrum represent the pectoral girdle.

INTERCLAVICLE: In every respect except its anterior margin the interclavicle is typical of the rhachitome type. The element is strongly ornamented ventrally and has a dorsally shallow concave curvature. The posterolateral borders are gently concave, whereas the anterolateral borders are straight and converge at a very shallow angle. The lateral corners are wide transversely over about one-third of the

bone length so as to form broad wings. The anterior border is not present, but there is no indication of any anterior constriction. The anterior edge was probably broad and straight. Ridge impressions indicate that there may have been a pectinate extension of the anterior margin as in the type.

The interclavicle clearly shows wide, low-ridged impressions for the clavicles on its wings and anterolateral margins. These impressions become narrow and pinch out altogether at least 5 to 7 mm. from the anterior margin. Anteromedially, there is a broad ornamented space (6 mm.) that separated the two clavicles.

CLAVICLE: The clavicles, also, are unremarkable, exhibiting no marked differences from other trimerorhachoids with the exception of a large foramen that punctures the element at its anterior tip. The elements are anteriorly oval in outline. The posterior border is wide and excavated. The lateral and medial borders are convex with a sharp convergence anteriorly. Posterolaterally, the dorsal process rises at a sharp angle from the body of the clavicle.

Both clavicles have their internal surface exposed. Striations run parallel to the anteromedial edge that mark the area overlapping the interclavicle. The anterior end is thickened and elevated above the rest of the bone which forms a shelf. This shelf continues along the lateral border to the posterolateral upwelling for the dorsal process. This upwelling indicates that the anterior tip of the bone was lateral to the interclavicle border. The posterior border extends about 2 mm. past the dorsal process. The length of the entire bone is about 24 mm.

CLEITHRUM: Only the descending stem (6 mm. with 2 mm. more as an impression) of the cleithrum lies open to view. The stem increases in diameter until it plunges into matrix below the overlying right clavicle. A prominent groove runs longitudinally for the reception of the anterodorsal edge of the scapula. The extent of the dorsal expansion over the scapula cannot be determined.

The large, shallowly curved interclavicle and clavicle and the sharp angle between the dorsal stem and main body of the clavicle indicate quite clearly a flat-bodied animal.

APPENDICULAR SKELETON

The appendicular skeleton is meagerly represented. Only a right humerus and one phalanx are present.

HUMERUS: The humerus is complete and is exposed dorsally. Both proximal and distal ends are expanded and completely developed. The two ends are twisted 46 degrees to one another. A similar degree of twist occurs in *Eryops* (KU 762). The type humerus has only a 10 to 15 degree twist. In the referred specimen most crests and processes are only slightly developed. There is no distinguishable supinator process. The pectoral crest turns sharply downward and curves moderately ventral to end in matrix level with the humerus waist. The sharp downward turn sets off the pectoral crest from the rest of the head. The long length and moderate curvature points toward a crest as strongly developed as in *Eryops*.

The articulating portion of the head is short, thin, and nearly straight, ending in a slightly curved knob. This knob must be the subcoracoscapularis process. It is developed to a similar degree in *Eryops*.

The proximal expansion constricts to a waist and then immediately expands distally. There is no shaft unlike the moderate one seen in the type. Slight ridges run distally from the waist toward the ectepicondyle and entepicondyle. A slight bump forms the end of the ectepicondyle. The distal end is triangular in shape with the anterior and posterior halves converging at right angles. Their intersection is emarginated to accommodate the olecranon process of the ulna. The entepicondyle extends much farther distally than the ectepicondyle as in *Eryops*.

The general outline of the humerus resembles that of *Eryops* except most areas for muscular attachment are not nearly so well developed. The poor development of muscle attachments indicates an animal adapted to an aquatic life. This agrees with the aquatically shaped flat clavicle and abruptly upturned dorsal process. However, the humerus is stout and relatively long compared to skull length. *Dvinosaurus* and *Trimerorhachis* are more primitive in still maintaining a weakly devel-

oped supinator process. The degree of twist in *Acropolous* is comparable to that in *Dvinosaurus* but less than in *Trimerorhachis*. The humerus of *Isodectes* is unknown, whereas the *Sauvagepeton* humerus is preserved but all features are obscured.

The only phalanx preserved is dorsoventrally compressed with the ends slightly expanded.

RIBS

Eight ribs are scattered over the block and none are in direct association with vertebrae. Five cervicals and three dorsal ribs are present. Neither of the two series is remarkable in any way. *Neldasaurus* shows similar dorsal ribs, whereas the cervicals resemble closely those described for *Gephyrostegus* (Carroll, 1970).

The cervical ribs are broad, anteroposteriorly compressed, and short. The head is differentiated into two distinct capitular and tubercular facets. The tuberculum is a long (4 mm.) narrow process which is a continuation of the dorsal margin of the rib. The capitulum in one rib is well developed (1.8 mm. long) and runs roughly parallel to the tuberculum. In other cervicals the capitulum projects only as a boss separated from the tuberculum base by a slight concavity. The capitulum articulated on the lower one-third of the posterior face of the intercentrum with the tuberculum lying just above the angle of the pedicel.

The total length of 14.1 mm. is only one and one-third times greater than the height of the neural arch. The shaft is wide proximally (3.0 mm.) but constricts at mid-length to a width of 2.1 mm. The shaft expands distally to a width of 2.8 mm. Part of the distal expansion forms a dorsally directed blade. The distal end is unfinished bone and presumably continued in cartilage. A low, narrow ridge traverses the ventral surface from the tubercular process down across the posterior face to the distal end of the bone. The anterior face of the rib is smooth with no irregularities.

The cervical ribs most likely ran posteroventrally with the anterior surface facing laterally. This orientation would allow the anterior surface to front the internal surface of the

scapula. The ribs may have overlain one another distally as evidenced by the longitudinal ridge and the small dorsal expansion at the distal end.

Where along the vertebral series the dorsal ribs belong cannot be determined. These are more like typical rhachitomous dorsal ribs with the capitulum and tuberculum forming a single, undivided head. The head is shaped so that the tuberculum is set off at an angle from the capitulum. Like the ribs, the shaft is anteroposteriorly compressed. The shaft remains fairly constant in width (2.4 mm.) up to the distal third of the bone where it gradually tapers. A groove runs along the dorsal edge of the proximal one-half of the rib.

Both dorsal ribs are incomplete and have a minimum length of 16.0 mm. so that they are slightly longer than the cervical ribs. The shaft is only slightly curved so that the ribs extend far laterally. The result is a dorsoventrally compressed body form. The ventral body width across the pectoral girdle is at least 35 mm. This figure agrees well with the rib length plus vertebral width (8 mm.) of 40 mm.

SCALES

Two types of scales are preserved. Pitted subround osteoderms fit well with similar structures on the type. Only isolated pieces are found throughout different layers of the matrix. A series of articulated scales lie on one small shale fragment (fig. 4b). The scales are much longer than wide (6 mm. to 2 mm.) with gently convex longitudinal borders. Each scale appears to overlap one-half of its neighbor. Very low ridges run longitudinally down the scales. The scales are very thin.

DISCUSSION

In this section I summarize the similarities between the type and referred specimens of *Acropelous vorax* so as to establish that they are conspecific. Further, and more importantly, I attempt (1) a precise placement of *Acropelous* within the saurerpontontids; (2) the relation of this group to the brachyopids; and (3) an analysis of all characters used in a hypothesis of relationships with respect to other rhachitomous amphibians.

The similarities of the referred specimen to the type leave no doubt that they are the same species. The skull roof is nearly identical with that of the type (fig. 2). The wide overlap of some of the skull roof elements could easily account for the small differences seen in ventral and dorsal views. The humerus exhibits the largest difference between the specimens but this is due to increased maturity. Hotton (1959) stated that "ossification in most of the . . . limb bones is restricted to perichondral layers . . ." Because the new specimen is more mature, more periosteal bone is deposited, giving the bone its larger size and better developed articular surfaces and processes.

The largely cartilaginous pleurocentra are probably larger than intercentra in the referred specimen. The vertebrae as preserved only represent the ossified portions of the column. Presumably, the type pleurocentra were also continued in cartilage to a greater overall size than the intercentra. The neural arches lie at a flatter angle on the centra as indicated by the poorly developed posterior zygapophyses. Comparison to the type in this regard is difficult because only two partial neural arches are exposed. Nothing of its structure contradicts the new interpretation.

The pterygoid of both specimens is identical except for size. The dorsal margin of epityrgoid, conical recess, and deep vertical shelf of palatine ramus agree completely. The anteriormost part of the palatine ramus has a slightly wider horizontal shelf in the type. However, the anterior part of the vertical shelf could have been crushed into the horizontal plane. The ventral half of the quadrate ramus in the type is missing.

The clavicles prove to be more broad than illustrated for the type. This may be due to differences in relative growth of the larger (referred) specimen.

Both lower jaws, basisphenoid, cervical ribs, and neural arches add more information about *Acropelous vorax*. However, these structures are either not present or incomplete in the type and do not invite comparison between the specimens.

Placement of *Acropelous* within the Trimerorhachoidea has been established by Chase (1965). Advanced characters used by Chase are:

(1) antorbital flattening; (2) small otic notch; (3) "postorbital segment of skull expanded"; (4) short faced; (5) "quadrate close to the level of the occipital condyle"; (6) "broad cultriform process of the parasphenoid"; (7) "anterior palatal fenestrae"; (8) "modest retroarticular process in the lower jaw."

Previous to Chase's work other workers were led astray by an earlier interpretation of *Saurerpeton* in which its synonym "Pelion" was thought to be a valid genus. Steen (1931) and Watson (1956) had misinterpreted the anterior palatal fenestrae of "Pelion" for internal nares. As a result Hotton (1959) followed Steen and hypothesized two parallel lineages of trimerorhachoids. He attempted to place *Acropelous* in a line between *Saurerpeton* and *Dvinosaurus* largely on the presence of symphyseal tusks and anterior palatal fenestrae. Hotton's other line consisted of "Pelion"—"Eobrachyops"—brachyopids. Hotton thought these three genera lacked symphyseal tusks and anterior palatal fenestrae, and thus were closely related. Chase established that symphyseal tusks and accompanying palatal fenestrae are present in all adequately known trimerorhachoids. Therefore, no dichotomy between a *Trimerorhachis*—*Acropelous* line and "Pelion"—"Eobrachyops" line existed. Instead, *Acropelous*, "Eobrachyops," and *Saurerpeton* were placed in a new family, the Saurerpetontidae. This study corroborates Chase's hypothesis that these three genera, including the newly described *Kourerpeton* (Olson and Lammers, 1976) and the brachyopids, are more closely related to one another than to any other trimerorhachoid. Further, this study hypothesizes that *Dvinosaurus*, which Chase (1965) placed in a separate family, is the sister group to the Saurerpetontidae.

Figure 5 shows a hypothesis of relationship for *Trimerorhachis*, *Dvinosaurus*, the saurerpetontids, and the brachyopids. One can see from figure 5 that the saurerpetontids are paraphyletic, for they exclude their sister group, *Kourerpeton* plus the brachyopids. The numbers at the nodes of the cladogram refer to characters which appear in table 1. Each character is thought to be apomorphic at the level in which it appears. The characters are discussed separately below. Characters 1-6 are apomorphies

which unite trimerorhachids, *Dvinosaurus*, saurerpetontids, and brachyopids as a monophyletic group (however, see discussion of character 4, below). It is not known whether or not trimerorhachoids are monophyletic but are shown to be such in figure 5. It is beyond the scope of this paper to attempt to test the hypothesis that they are monophyletic. Character 1 (otic notch poorly developed) occurs in the group listed in figure 5 and in *Otocratia* (Watson, 1929), *Colosteus* (Romer, 1930), *Erpetosaurus* (Romer, 1930), *Tertrema* (Romer, 1947), *Cyclotosaurus* (Fraas, 1889), and metoposaurs (Sawin, 1945). *Tertrema* and *Cyclotosaurus* secondarily close the otic notch but an opening is still present. The condition is not comparable to trimerorhachoids. The metoposaurs may be closely related to the brachyopids (Romer, 1947) and this is not a valid outgroup. The other genera are unrelated to one another, and presumably do not represent the primitive condition for temnospondyls.

Character 2 (expanded postorbital region) occurs in the groups listed in figure 5, *Colosteus* (Romer, 1930), *Erpetosaurus* (Romer, 1930), various trematosauers (Meyer, 1858; Huene, 1920), plagiosaurs (Watson, 1956), and metoposaurs (Fraas, 1889; Case, 1922; Branson and Mehl, 1929). We see that only two primitive types possess an expanded postorbital region. Trematosauers are not primitive labyrinthodonts and their systematic position within the group is uncertain. Metoposaurs and plagiosaurs (Romer, 1947; Watson, 1956) may be close relatives to the brachyopids. These groups, then, do not constitute valid outgroups.

Character 3 (broad cultriform process) occurs in many other labyrinthodonts besides those in figure 5. The only primitive type with a broad cultriform process is *Eugyrinus* (Watson, 1921). Various eryopids such as *Eryops* (Sawin, 1941), *Platyrhinops* (Steen, 1931), *Stegops* (Romer, 1930; Steen, 1931) have a moderate to broad cultriform process. It also occurs in more advanced rhachitomes such as the trematosauers *Lyrocephalus* (Save-Soderbergh, 1935), and *Peltostega* (Wiman, 1916), the neorhachitomes *Lydekkerina* (Watson, 1919) and *Sclerothorax* (Huene, 1932), and various capitosauers (Meyer, 1858; Welles and Cosgriff, 1965). Again, the metoposaurs (Case, 1922;

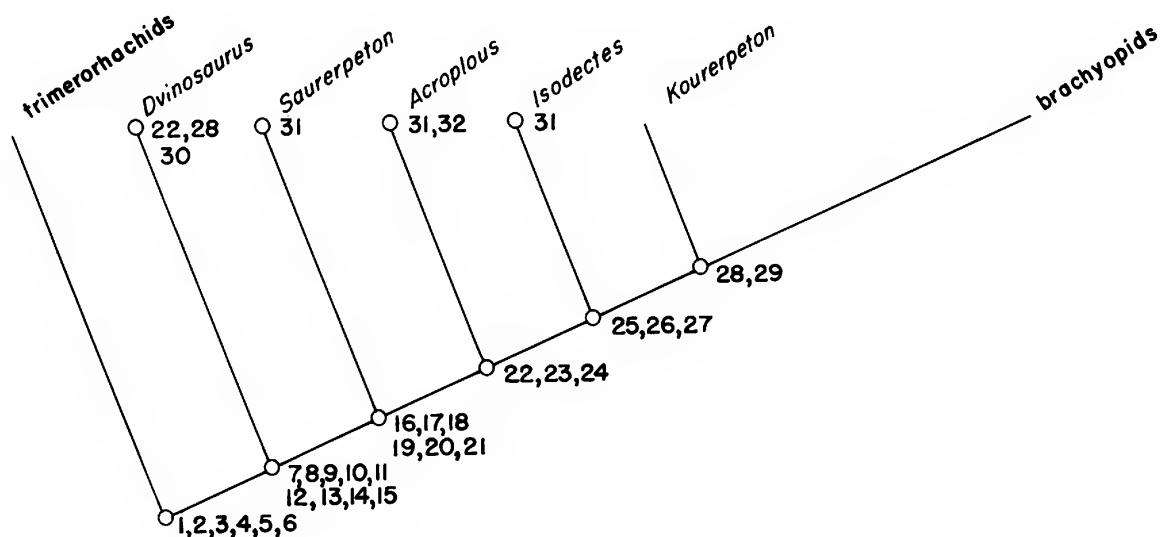


FIG. 5. A hypothesis of relationships that unite trimerorhachids, *Dvinosaurus*, saurerpetontids (*Saurerpeton*, *Acropelous*, and *Isodectes*), *Kourerpeton*, and brachyopids as a monophyletic group. The numbers refer to derived characters listed in table 1.

Branson and Mehl, 1929) and plagiosaurs (Huene, 1922) show this character. Because only one primitive form (*Eugyrinus*) possesses the broad cultriform process it is thought to be derived for the trimerorhachoids. These other advanced groups which show it could be argued to be closely related to trimerorhachoids, but this would rely on a parsimony argument. All that can be shown here is that character 3 tends to unite the groups in figure 5 as a monophyletic group.

Character 4 (paired anterior palatal fenestrae) occurs in very few labyrinthodont genera besides those appearing in figure 5. Genera such as *Trematosuchus* (Haughton, 1925), *Platystega* (Wiman, 1915), *Tertrema* (Wiman, 1917), *Trematosaurus* (Watson, 1919), *Kestrosaurus* (Haughton, 1925), and *Mastodonsaurus* (Fraas, 1889) also show character 4. All other genera that show anterior palatal fenestrae have median unpaired vacuities. The character as it appears in the latter two genera is probably not homologous on grounds of topographic dissimilarity. Metoposaurs show paired anterior palatal fenestrae and may be closely related to the trimerorhachoids. Because only a few other genera show character 4, the character is probably advanced and unites trimerorhachoids as a

natural group. Brachyopids, however, show what looks like the primitive condition of median unpaired fenestrae. To maintain the present hypothesis one must argue that brachyopids secondarily fused the fenestrae independently of other groups that also show the character. This ad hoc hypothesis weakens the hypothesis of relationships shown in figure 5.

Character 5 (retroarticular process moderate in length) occurs in every taxon of figure 5 in which the lower jaw is well enough known. The character appears in few other temnospondyls except most stereospondyls (Nilsson, 1944). Among more primitive rhachitomes the character occurs in *Cacops* (Case, 1911) and *Eugyrinus* (Nilsson, 1944). Most primitive forms lack any retroarticular process such as the ichthyostegids, loxomids, and colosteids (where known). Regardless of the condition in stereospondyls, the character is considered to be derived.

Character 6 (moderately developed medial exposure of angular) is found in only one primitive rhachitome, *Megalocephalus*. Nilsson (1943) stated that this condition is advanced for the stegocephalia. Advanced taxa, besides those in figure 5, which also show the character are *Sassenisaurus* (Nilsson, 1943), a capitosaur,

and *Aphaneramma* (Nilsson, 1943), a trematosaur. Within the trimerorhachoids, the condition is unknown in *Kourerpeton*. *Saurerpeton* (AMNH 6935) shows very clearly a narrow medial exposure of the angular. The contribution of angular in *Isodectes* is similar, but from Watson's (1956) figures it could have been no more than is seen in brachyopids. This study shows the same condition in *Acropelous*. Among brachyopids, *Blinosaurus* (Cosgriff, 1969), *Hadrokkosaurus* (Welles and Estes, 1969), and *Boreosaurus* (Nilsson, 1943) also show the character. A narrow medial exposure of the angular seems to be derived for trimerorhachoids.

Characters 7 through 15 are used here to

unite *Dvinosaurus*, saurerpetontids, and brachyopids as a monophyletic group.

Character 7 (antorbital flattening) is very marked in these forms. A relatively deep snout occurs in primitive rhachitomes such as *Ichthyostega* (Save-Soderbergh, 1932), *Colosteus* (Romer, 1930), *Macrerpeton* (Romer, 1930), and *Dendrerpeton* (Steen, 1934). The status of this character as being derived depends on the meager reconstructions available being both accurate and representative.

Character 8 (broad parabolic outline of skull in dorsal view) occurs in very few other rhachitomes other than those of figure 5. *Amphibamus* (*Potamochastus* Steen, 1938) and *Stegops* (Romer, 1947) have similar skull roof

TABLE 1
Apomorphic Characters Appearing in Figure 5

1. Otic notch poorly developed.
2. Expanded postorbital region.
3. Broad cultriform process.
4. Paired, anterior palatal fenestrae.
5. Retroarticular process moderate in length.
6. Moderately developed medial exposure of angular.
7. Antorbital flattening.
8. Broad parabolic outline of skull in dorsal view.
9. Modest ventrally directed flange of quadrate process of pterygoid.
10. Space separating pterygoid from squamosal in occipital view.
11. Narrow lateral exposure of splenials.
12. Squamosal and quadratojugal cover the posterior surface of quadrate.
13. Occiput projects posterior to skull roof.
14. Double occipital condyle.
15. Lateral wing of parasphenoid articulates on ventral shelf of pterygoid.
16. Small palatal teeth absent.
17. Maxilla fails to reach level of anterior border of subtemporal fossa.
18. Quadrate anterior to occipital condyle.
19. Cheek deep posteriorly with quadrate well below parasphenoid.
20. Palatine enters border of interpterygoid vacuities.
21. Well-developed coronoid process.
22. Pronounced ventrally directed flange of quadrate process of pterygoid.
23. Further reduction of otic notch.
24. Vagal foramen completely enclosed by exoccipital.
25. Palatine-vomer contact lateral to choanae.
26. Otic notch lost.
27. Antorbital flattening more pronounced.
28. Intertemporal lost.
29. Fusion of braincase and palate.
30. Posterior coronoid forms distinct pillar like coronoid process.
31. Tabulars reduced to narrow strips.
32. Wide lateral exposure of both splenials.

outlines. Because these genera are not closely related to the taxa under study, the character is considered derived.

Character 9 (modest ventrally directed quadrate process of pterygoid) occurs in no other group of labyrinthodonts. Some temnospondyls have a stout and deep quadrate process of the pterygoid (*Megalcephalus*, *Eryops*, *Edops*, Romer 1947), but in none of these does the process form a sharp angle with the rest of the pterygoid. This character, then, is thought to be derived for *Dvinosaurus* and its more apomorphous sister groups.

Character 10 (space separating pterygoid from squamosal in occipital view) is used here only tentatively. The character is unknown in *Saurerpeton*, *Acropelous*, and *Kourerpeton*. However, it does occur in *Dvinosaurus* (Bystrow, 1938), *Isodectes*, and brachyopids (Watson, 1956). Among other temnospondyls *Platystegos* (Watson, 1956), *Platyops* (Efremov, 1933), and *Trematosaurus* (Jaekel, 1922) show the character. Except for *Platystegos* and primitive forms well enough known (loxomids, *Edops*, Romer and Witter, 1942) the pterygoid is closely appressed against the squamosal.

Character 11 (narrow lateral exposure of splenials) is found in only one primitive form, *Eugyrinus* (Watson, 1940) besides those taxa which share it in figure 5. Other temnospondyls which show the character are *Eryops* (Sawin, 1941) and stereospondyls (Nilsson, 1943). *Acropelous*, as can be seen in figure 1, has a wide lateral exposure of both splenials (character 32). This is a clear contradiction to the hypothesis of relationships of figure 5. Because this is the only taxon that does not share the derived state it is considered to be a character reversal and hence an autapomorphy. However, considering the wide lateral exposure of splenials in *Acropelous* as an autapomorphy is an ad hoc hypothesis used to save the general hypothesis of relationships. Hence, regardless of what one calls the condition in *Acropelous*, the general hypothesis is weakened.

Dvinosaurus has no separate intertemporal (character 28). This would tend to unite *Dvinosaurus* with *Kourerpeton* and the brachyopids since this is a derived character.

To accept *Dvinosaurus* as the sister group to the saurerpetontids, *Kourerpeton*, and brachyopids requires the ad hoc hypothesis that the intertemporal was lost independently in *Dvinosaurus*. Bystrow (1938) suggested that the postorbital may be a compound element. However, in all of Bystrow's illustrations the ornament pattern radiates from the center of the postorbital out to its periphery. One sees no hint of two centers of ornament radiation or any other sign that the element may be compound.

Chase (1965) mentioned other special characters in which *Dvinosaurus* is presumed to be advanced over most other trimerorhachoid genera. The exoccipital completely surrounds the vagal foramen as in *Isodectes* and *Kourerpeton*. The condition is unknown in *Saurerpeton* and its position is only guessed at in *Acropelous*. Another supposed advanced character is the tabular contributing to the paroccipital bar. The new specimen of *Acropelous* shows the same condition. Again, however, the condition is unknown in *Saurerpeton*. Because of our spotty knowledge of the distribution of these features they cannot contradict the present hypothesis of relationships.

Character 12 (squamosal and quadratojugal cover posterior surface of quadrate) occurs in only one other genus (*Platystegos*, Watson 1956) besides *Dvinosaurus* (Watson, 1956) and its more apomorphic sister taxa. However, the condition is unknown in both *Saurerpeton* and *Acropelous*. Olson and Lammers (1976) stated that in *Kourerpeton* "the quadratojugal and squamosal carry around the quadrate posteriorly, but only slightly . . ." Regardless of its degree of expression, I regard the character as present in this genus.

Character 13 (occiput projects posterior to skull roof) is found only in those taxa in figure 5 except possibly *Kourerpeton* (Olson and Lammers, 1976). The character is also questionable in *Saurerpeton*, although Watson (1956) illustrated the occiput of "Pelion" sloping posteriorly away from the skull table. *Metoposaurus* (AMNH 1832) and *Gerrothorax* (AMNH 3868) also show the character. Because the metoposaurs and plagiosaurs are probably closely related to the brachyopids

(Romer, 1947), they do not constitute a valid outgroup. Therefore, the character is judged to be derived for *Dvinosaurus* and its sister group.

Character 14 (double occipital condyles) occurs in *Dvinosaurus*, brachyopids, and probably *Acropelous*. The condition is unknown in *Kourerpeton* (Olson and Lammers, 1976). It was always assumed that *Saurerpeton* showed the primitive condition. However, specimen USNM 4471 shows what may be a ventrally exposed exoccipital which carries a fairly wide posteriorly facing surface. It cannot be seen whether this surface is finished or was continued in cartilage. At any rate the element looks very much like the exoccipital of *Acropelous*. The condyle may have been double. Other specimens give further suggestive evidence of a double condylar condition. A specimen of *Saurerpeton* (AMNH 6837) shows a smooth occipital surface, but to one side of the midline a boss raises up toward the ventral surface of the occiput. This boss faces posteriorly and ends in unfinished bone.

These two specimens are very suggestive of the condition in *Acropelous*. It is entirely possible that the unfinished surfaces in the latter specimen were completed in two separate cartilaginous condyles. In no specimen of *Saurerpeton* was there any suggestion of a single occipital condyle.

Watson (1956) stated positively that *Isolectes* possesses a single "large, concave condyle." After reexamination of the type (AMNH 2455) all one can say of the basioccipital area is that a fairly large area of fractured and possibly unfinished bone exists. Dorsally, the exoccipitals form raised pillars that support large unfinished and posteriorly facing bosses on lateral sides of the foramen magnum. Exactly as in *Acropelous* and *Saurerpeton* these bosses could have supported double cartilaginous condyles. However, given the relatively large area presumably filled by the basioccipital, a single condyle could also have been present. Because we simply do not know what the condition is in these three genera this character must be considered primitive.

Character 15 (lateral wing of the parasphenoid articulates on the ventral shelf of the pterygoid) is a distinct character which is

plainly seen in *Dvinosaurus* (Amalitsky, 1921; Bystrow, 1938), *Saurerpeton* (AMNH 6928, USNM 4471, PU 19298) and *Isolectes* (AMNH 2455). In all of these specimens the anterior margin of the parasphenoid body abuts against a posteriorly facing wall of the internal process of the pterygoid. Dorsally, a shelf covers the anterolateral portion of parasphenoid. In *Acropelous*, Hotton (1959) has reconstructed the parasphenoid and pterygoid in an identical fashion. Only the dorsal view of the internal process of the pterygoid can be seen in the present specimen (KU 28352). Both *Kourerpeton* and brachyopids fused the parasphenoid with the pterygoid. The complete fusion of the palate to the braincase in these two taxa in no way contradicts the hypothesis of relationships given in figure 5. On the other hand, because different character states are involved, they cannot corroborate the hypothesis either.

Among different forms *Dendrerpeton* (Watson, 1956; Carroll, 1967) and *Erpetosaurus* (Romer, 1930; Watson, 1956) share this character. Among more advanced forms *Actinodon* (Watson, 1962) shares this character. *Erpetosaurus* is a colosteid and if that taxon constitutes the sister group to the trimerorhachoids then character 15 may be primitive within the saurerpetontids. However, because it is not seen in all other primitive temnospondyls, and its distribution is not well known within the colosteids, the character is used as a synapomorphy. Obviously, in light of its distribution in other temnospondyls, its assignment as being derived can only be tentative.

Characters 16 through 21 unite *Saurerpeton*, *Acropelous*, *Isolectes*, *Kourerpeton*, and brachyopids as a monophyletic group. Character 16 (small palatal teeth lost) is a weak character in that its distribution throughout the rhachitomes makes its derived status questionable. In nearly all primitive rhachitomes, palatal teeth (exclusive of the shagreen of very small denticles) are restricted to tusk pairs on the palatal elements. In *Neldasaurus*, *Trimerorhachis*, and *Dvinosaurus* a large number of small teeth grow in line with the larger tusks. One cannot use character 16 to corroborate the hypothesis in figure 5 with the present knowledge of its distribution within the trimerorhachoids. The

character can only be derived if *Trimerorhachis*, *Neldasaurus*, and *Dvinosaurus* are primitive sister groups. Obviously, by using these three genera as an outgroup, character 16 must be derived and hence corroborate the hypothesis of relationships. If these three genera are more closely related to any of the "saurerpetontids" or brachyopids, then character 16 would be primitive and could not corroborate the present hypothesis.

Character 17 (maxilla fails to reach level of anterior border of subtemporal fossa) is found in specified taxa in figure 5 and in cheiroprosopids (Romer, 1947). The character also occurs in the capitosaur *Stenotosaurus* (Romer, 1947). The maxilla in the brachyopid *Bothriiceps* just reaches the anterior margin of the subtemporal fossa. The metoposaur *Metoposaurus* also shows the condition seen in *Bothriiceps*. Because primitive rhachitomes do not show the character (*Ichthyostega*, Save-Soderbergh, 1932; *Erpetosaurus*, Romer, 1930; loxomids, Watson, 1929; *Edops*, Romer and Witter, 1942; *Dendrerpeton*, Carroll, 1967; *Eugyrinus*, Watson, 1940; *Eryops*, Sawin, 1941) as well as some advanced forms such as trematosaurs and capitosaurs (just mentioned), the character is thought to be derived. This judgment is made in spite of some brachyopids and metoposaurs showing an intermediate condition.

Character 18 (quadrate anterior to occipital condyles) occurs in no known primitive rhachitome. Besides those taxa in figure 5, metoposaurs (Fraas, 1889; Case, 1922; Branson and Mehl, 1929), some trematosaurs (*Lyrocephalus* and *Aphaneramma*, Romer 1947) and the capitosaurid *Cyclotosaurus* (Meyer, 1858; Fraas, 1889; Welles and Cosgriff, 1965) show the same condition. Because these latter taxa do not constitute the primitive sister taxa to those listed in figure 5, the character is concluded to be derived.

Character 19 (cheek deep posteriorly with quadrate well below paraspheonoid) can be seen quite clearly in saurerpetontids, *Kourerpeton*, and brachyopids. These taxa have ratios of quadrate width vs. height of paraspheonoid above the base of the quadrate of 5.6 or less. *Trimerorhachis* (Watson, 1956) and

Dvinosaurus (Bystrow, 1938) have ratios of 70.0 and 7.9, respectively. In *Neldasaurus* (Chase, 1965) the quadrate is actually above the paraspheonoid. If these three genera are more primitive sister groups of *Saurerpeton* and its close relatives, then this character is derived. However, primitive rhachitomes in general have low ratios such as *Megalcephalus* (Romer, 1947) and *Dendrerpeton* (Romer, 1947). As for character 19 the distribution of high ratio taxa within nonsaurerpetontid trimerorhachoids would have to be known in order to assign the character as derived.

Character 20 (palatine enters border of interpterygoid vacuities) occurs in nearly every group of advanced temnospondyls besides those of figure 5. There is no doubt that it is an advanced character for in no primitive form does the palatine enter the vacuities.

Character 21 (well-developed coronoid process) is discussed at this point only tentatively. One specimen of *Saurerpeton* (AMNH 6935) shows a well-developed coronoid process. This bulge behind the dentary, however, could be due to post-mortem crushing and flattening. *Acropelous*, *Isodectes* (Watson, 1956), and brachyopids have moderate (*Hadrokosaurus*, Welles and Estes, 1969) to well-developed (*Blinosaurus*, Cosgriff, 1969) coronoid processes. The condition in *Kourerpeton* is unknown. *Dvinosaurus* also has a pronounced coronoid process but it is formed in a different way. The posterior coronoid forms a distinct pillar-like coronoid process (character 30). It is judged to be nonhomologous with character 21 and, thus, cannot contradict the hypothesis of relationships.

Characters 22 through 24 unite *Acropelous*, *Isodectes*, *Kourerpeton*, and brachyopids as a natural group. Character 22 (pronounced ventrally directed flange of quadrate process of pterygoid) can be seen clearly in brachyopids, *Acropelous*, and *Isodectes*. The quadrate flange of pterygoid in *Kourerpeton* does not bend ventrally to the same degree as in the former taxa. The condition in *Kourerpeton*, then, contradicts the hypothesis of relationships. It is required to erect an ad hoc hypothesis that *Kourerpeton* secondarily lost the more pronounced condition.

Character 23 (further reduction of otic notch) is very distinct in *Acroploous* and its apomorphous sister groups. *Dvinosaurus* (Bystrow, 1938) shows the same condition. Again, it is necessary for the current hypothesis to hold, to assume that *Dvinosaurus* secondarily lost a deeper embayment of the otic notch. Very few forms approach the condition seen in *Acroploous* and its close relatives. *Cyclotosaurus* (Fraas, 1889) and some other cyclotosaurs secondarily close the notch from behind. Panchen (1972) argued that an unnotched skull roof may be primitive for the tetrapods. However, the otic notch surely must be primitive for the temnospondyls as a whole because nearly every taxon possesses it. In that case, its absence or reduction would be a derived condition.

Character 24 (vagal foramen completely enclosed by exoccipital) is used with uncertainty to unite *Acroploous*, *Isodectes*, *Kourerpeton*, and brachyopids. The condition is unknown in *Acroploous*, and Hotton (1959) restored the vagal foramen between the exoccipital and opisthotic. Given the evidence at hand, the vagal foramen could very well have laid entirely within the exoccipital. If *Acroploous* does not show this derived condition, then character 24 can be used to unite only *Isodectes*, *Kourerpeton* and brachyopids. As with many other characters in this study, character 24 occurs in other groups of stereospondyls (Romer, 1947). This type of character distribution will be discussed at the end of this section.

Characters 25 through 27 unite *Isodectes*, *Kourerpeton*, and brachyopids as a monophyletic group. Character 25 (palatine-vomer contact lateral to choana) occurs in only two genera (*Platyrhinops*, Steen 1931; *Metoposaurus*, Case 1922) besides those taxa mentioned in figure 5. The maxilla forms the external border of the choana in primitive forms. This character, then, must be derived.

Character 26 (otic notch lost) is unique among the group including *Isodectes*, *Kourerpeton* and brachyopids. As mentioned before, capitosaurs such as *Cyclotosaurus* (Fraas, 1889) have no posterior emargination of the skull roof but this condition is fundamentally different than in taxa of figure 5.

Character 27 (antorbital flattening more pro-

nounced) as seen in Watson's (1956) and Welles and Estes' (1969) figures shows that *Isodectes* and brachyopids are very distinct. However, *Kourerpeton* has as deep a snout as *Acroploous*. Also, capitosaurs, metoposaurs, and trimerorhachids such as *Neldasaurus* and *Trimerorhachis* exhibit character 27 as well. This character, then, can be used only tentatively to unite *Isodectes*, *Kourerpeton*, and brachyopids.

A possible contradiction of the present hypothesis must be dealt with here. *Saurerpeton*, *Acroploous*, and *Isodectes* have tabulars reduced to narrow strips (character 31). This character is not seen in brachyopids (the condition in *Kourerpeton* is unknown). If the present hypothesis of relationships were true, one would expect *Kourerpeton* and brachyopids to inherit the character from the common ancestor of *Saurerpeton* and brachyopids. To maintain the present hypothesis one must argue that narrow tabulars are either evolved independently in *Saurerpeton*, *Acroploous*, and *Isodectes*, or that the character was lost in brachyopids. Both alternatives are nonparsimonious and tend to contradict the present hypothesis. One could abandon the hypothesis as shown in figure 5 and unite *Acroploous*, *Saurerpeton*, and *Isodectes* as a monophyletic group (fig. 6).

Characters 28 and 29 unite *Kourerpeton* and brachyopids as a natural group. Unfortunately, the loss of the intertemporal (character 28) and fusion of the braincase and palate (character 29) occur in many other advanced temnospondyls (Romer, 1947).

There are no known derived characters uniting brachyopids exclusive of *Kourerpeton* as a natural group. Therefore, some brachyopids may be the sister taxa to both *Kourerpeton* and the remainder of the brachyopids. In other words *Kourerpeton* may be more closely related to a subunit of the brachyopids than to the brachyopids as a whole.

SUMMARY

A concise, testable hypothesis of saurerpetontid and brachyopid relationships has been presented. As one must have noticed, many characters (i.e., 2, 3, 4, 5, 6, 10, 11, 14, 17, 18, 20, 23, 24, 27, 28, 29) are not seen only in

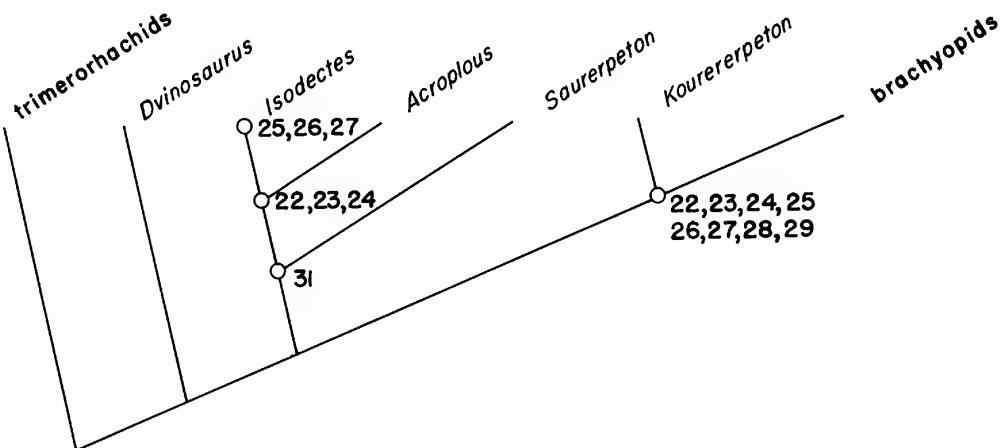


FIG. 6. Same hypothesis of relationships as in figure 5 except the saurerpetontids are considered to be a monophyletic group. This hypothesis is contradicted by the distribution of derived characters 22 through 27 and is thus contradicted more times than the hypothesis shown in figure 5. The numbers refer to derived characters listed in table 1.

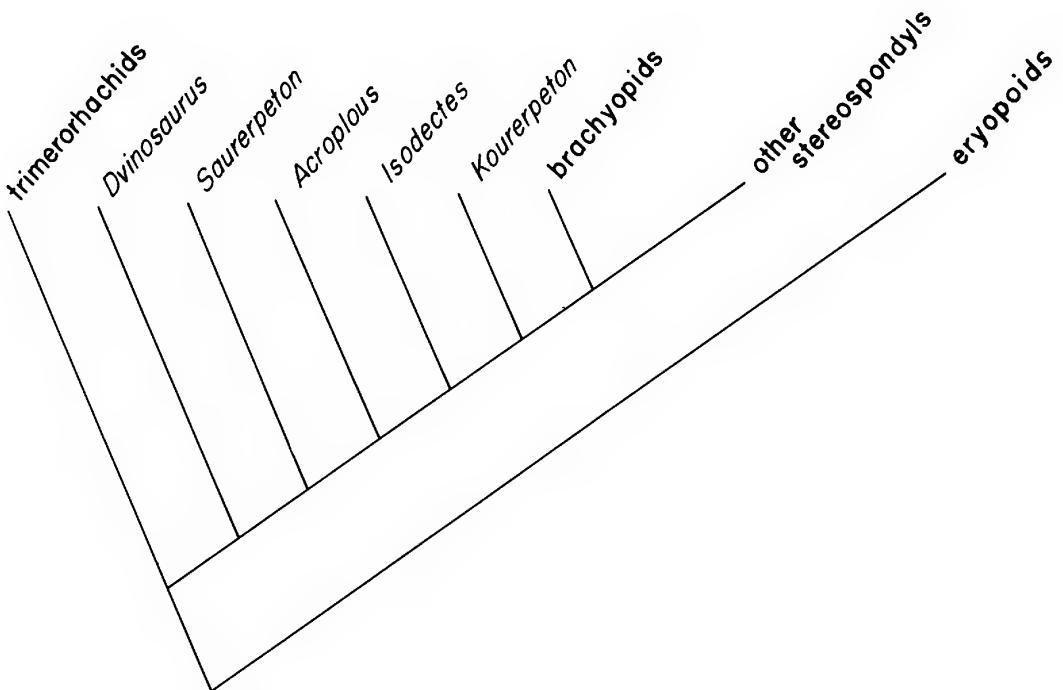


FIG. 7. A hypothesis of relationships uniting all stereospondyls with trimerorhachids, *Dvinosaurus*, *Saurerpeton*, *Acropelous*, *Isodectes*, and *Kourerpeton* as a monophyletic group exclusive of the eryopoids.

those taxa appearing in figure 5 but in other advanced temnospondyls (Romer, 1947). Given this distribution of characters, three alternative hypotheses of relationship exist. First, all stereospondyls are more closely related to the taxa in figure 5 than to eryopoids (fig. 7). Second, *Kourerpeton* and brachyopids could be more closely related to eryopoids than to tri-

merorhachids. Third, the trimerorhachids, *Dvinosaurus*, *Isodectes*, *Acropelous*, *Saurerpeton*, and *Kourerpeton* are more closely related to the eryopoids than to the other stereospondyls.

merorhachids (fig. 8). Third, the characters listed above could be derived in parallel which implies that stereospondyls are not monophyletic. That is, brachyopids are more closely

related to saurerpetontids, whereas other stereospondyls are more closely related to eryopoids (fig. 9). Given the preponderance of characters linking saurerpetontids, *Kourerpeton*

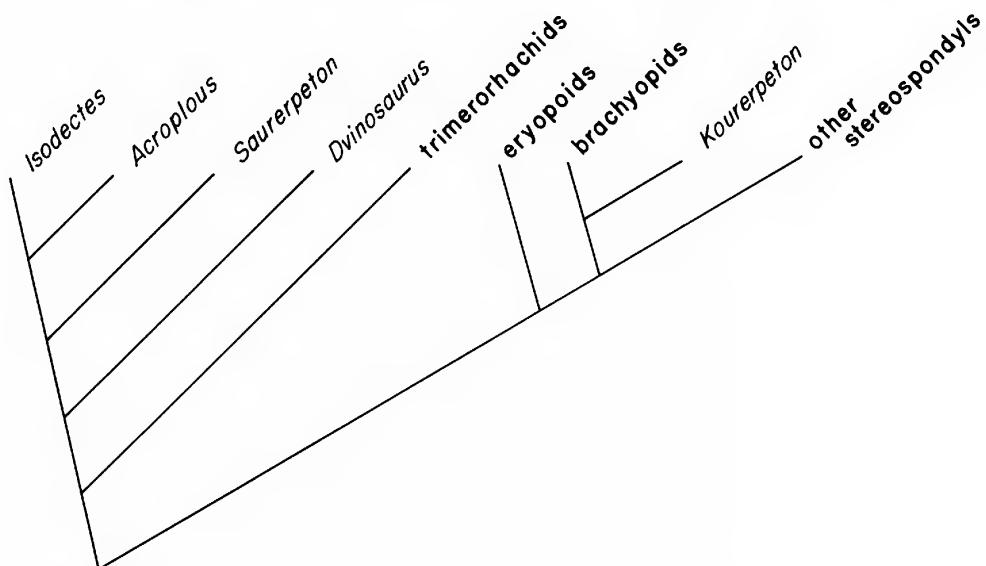


FIG. 8. A hypothesis of relationships uniting *Kourerpeton* and all stereospondyls with eryopoids as a monophyletic group exclusive of trimerorhachids, *Dvinosaurus*, *Saurerpeton*, *Acropelous*, and *Isodectes*.

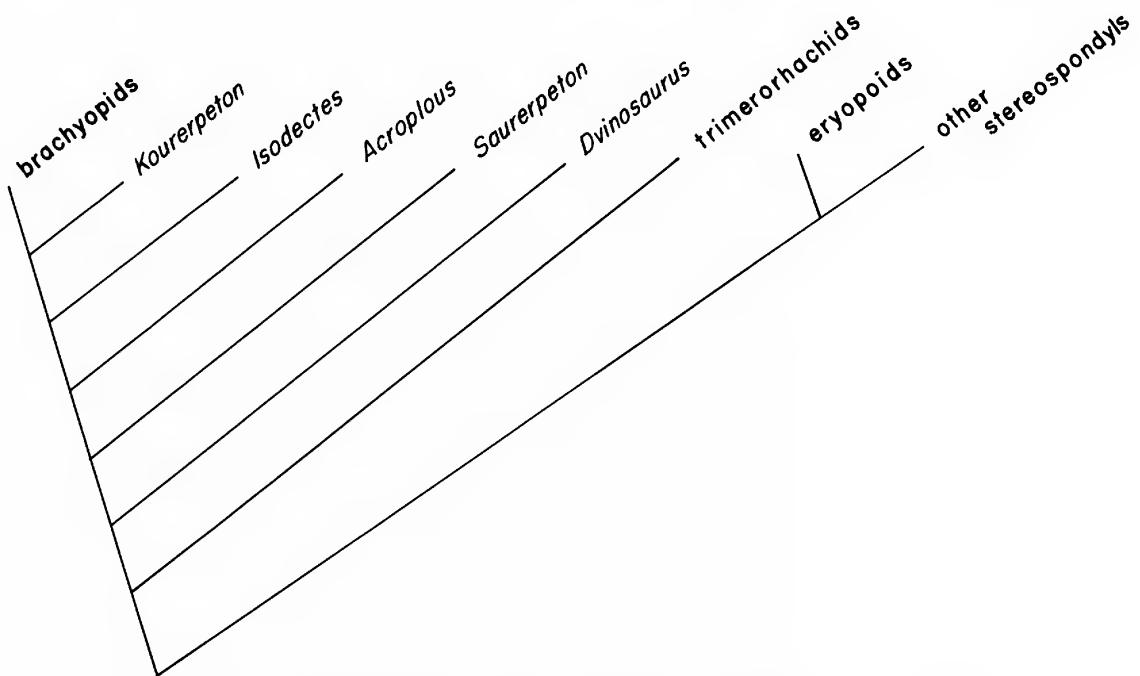


FIG. 9. A hypothesis of relationships showing stereospondyls to be polyphyletic.

and brachyopids as a natural group, the first or third phylogeny (figs. 7 or 9) seems to hold. For the phylogeny in figure 9 to hold, one would have to derive independently every character (except 28 and 29) between brachyopids and other stereospondyls and in trimerorhachids, *Dvinosaurus* and saurerpetontids. Given the present character distribution the hypothesis of relationships shown in figure 9 has been refuted. The conclusion that brachyopids are more closely related to saurerpetontids than to stereospondyls agrees with Watson (1956), Hotton (1959), Chase (1965), and Olson and Lammers (1976). Romer (1947) suggested that a close relationship might exist.

Unlike the authors just mentioned, I have tried to place *Dvinosaurus*, *Sauveterpeton*, and *Acropelous* in a clearer phylogenetic scheme. However, I have had no more success than Olson and Lammers (1976) concerning the position of *Kourerpeton*.

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